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Allium cytogenetics: a critical review on the Indian taxa

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Abstract

The genus *Allium* Linnaeus, 1753 (tribe Allieae) contains about 800 species worldwide of which almost 38 species are reported in India, including the globally important crops (onion, garlic, leek, shallot) and many wild species. A satisfactory chromosomal catalogue of *Allium* species is missing which has been considered in the review for the species occurring in India. The most prominent base number is x=8, with few records of x=7, 10, 11. The genome size has sufficient clues for divergence, ranging from 7.8 pg/1C to 30.0 pg/1C in diploid and 15.16 pg/1C to 41.78 pg/1C in polyploid species. Although the karyotypes are seemingly dominated by metacentrics, substantial variation in nucleolus organizing regions (NORs) is noteworthy. The chromosomal rearrangement between *A. cepa* Linnaeus, 1753 and its allied species has paved way to appreciate genomic evolution within *Allium*. The presence of a unique telomere sequence and its conservation in *Allium* sets this genus apart from all other Amaryllids and supports monophyletic origin. Any cytogenetic investigation regarding NOR variability, telomere sequence and genome size in the Indian species becomes the most promising field to decipher chromosome evolution against the background of species diversity and evolution, especially in the Indian subcontinent.

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Keywords
Allium, Chromosome, FISH, Genome size, Indian species, NORs, Telomere

Introduction

The genus *Allium* Linnaeus, 1753 is considered a wonder crop of global importance, catering to the agriculture, condiment, pharmaceutical, nutraceutical and cosmetic sectors of economy owing to the presence of numerous species with tremendous significance. Among several herb species, an onion (*A. cepa* Linnaeus, 1753) that is valued throughout the continent attracts a lot of attention of the economic sectors mentioned above, followed by garlics, leeks and shallots having limited uses. Onion is the second of the five main world vegetables species (after tomato) whose worldwide production accounted for 9% of the total (42–45%) increase in production of vegetables between 2000–2019 (https://www.fao.org/3/cb4477en/online/cb4477en.html#chapter-2_1).

Allium, previously referred to Liliaceae, is now a member of Amaryllidaceae sensu Angiosperm Phylogeny Group or APG III (Haston et al. 2009). This large genus (about 800 species, Costa et al. 2020) was divided into 15 subgenera and 56 sections (Friesen et al. 2006). At present, *Allium* has its primary evolution centre across the Irano-Turanian phytochorion while secondary centres of diversity include Mediterranean basin and western North America (Friesen et al. 2006). The taxonomy and evolution of this diverse genus has been accepted as difficult.

Cytogenetics, being the only elementary discipline of genetics, focuses on genome structure, function and evolution. The evolutionary history of organisms is inscribed in the chromosomes, the physically visible form of genome. The very fundamental parameters such as chromosome count reports, when combined with molecular cytogenetic and phylogenetic data (Islam-Faridi et al. 2020; Senderowicz et al. 2021), or genome size estimates, can elucidate trends of evolution in context of ploidy changes. Molecular cytogenetic approaches, in line with the parameters mentioned already, can accelerate the understanding of the evolutionary questions (Borowska-Zuchowska et al. 2022; Nath et al. 2022). A general correlation between evolutionary trends and chromosomal features has been shown in many plant families (Van-Lume et al. 2017; Carta et al. 2020; Bhowmick and Jha 2022; Nath et al. 2022). Recently, a broad concurrence between karyology and geographical distribution has been shown in three Allioidae tribes, with respect to the diversification of Allieae to Northern Hemisphere from the Indian tectonic plate around 30 million years ago (Costa et al. 2020).

India is the world's second-largest producer of onion after China, with a production rate of 16360 kg/ Ha (2020–2021) (https://eands.dacnet.nic.in/). After onion, *A. sativum* Linnaeus, 1753 (garlic) is the second largest species of *Allium* contributing significantly to agro-economical development of the country (https://eands.dacnet.nic.in/). Among the other species, *A. schoenoprasum* Linnaeus, 1753 and *A. roylei*

Stearn, 1947 exhibited resistance qualities (Nanda et al. 2016) and promise adoption of advanced breeding. Keeping in mind the significance of *Allium* and the complications in taxonomy and evolution, a comprehensive summary of cytogenetic characters has been presented for Indian species of *Allium*.

Data compilation

Distribution of taxa, chromosome counts, ploidy, karyotypes and molecular cytogenetic reports have been compiled from original publications, chromosome atlases and databases e.g. Database on Genome-Related Information of Indian Plants or d-GRIP (http://indianpcd.com/; Jha et al. 2019), Index to Plant Chromosome Numbers or IPCN (http://www.tropicos.org/project/ipcn, Goldblatt and Lowry 2011), Chromosome Counts Database or CCDB (http://ccdb.tau.ac.il/, Rice et al. 2015), The Plant DNA C-values database (https://cvalues.science.kew.org/, Pellicer and Leitch 2020) and Plant rDNA Database (www.plantrdnadatabase.com, Vitales et al. 2017). In case of synonyms, the present taxonomic designations are retained with appropriate references.

Cytogenetic catalogue of *Allium* species in India

There are 35–40 species of *Allium* currently reported from India (ca. 38 species) (d-GRIP, Pandey et al. 2021, 2022). The species of *Allium* in India belong to nine subgenera namely, *Cepa* (5 species), *Allium* (5 species), *Amerallium* (4 species), *Reticulatobulbosa* (3 species), *Polyprason* (3 species), *Anguinum* (2 species), *Butomissa* (2 species), *Melanocrommyum* (1 species) and *Rhizirideum* (2 species) (Friesen et al. 2006). Majority of the *Allium* species prefer temperate mixed forests or rocky slopes ranging 1200–5480 meters of the western Himalayas (e.g. *A. atropurpureum* Waldst. et Kit., 1800, *A. atrosanguineum* Schrenk, 1842, *A. auriculatum* Kunth, 1843, *A. caesioides* Wendelbo, 1969, *A. carolinianum* Redouté, 1804, *A. consanguineum* Kunth, 1843, *A. fedtschenkoanum* Regel, 1875, *A. griffithianum* Boiss., 1859, *A. loratum* Baker, 1874, *A. oreoprasum* Schrenk, 1842, *A. roylei*, *A. schoenoprasum* and *A. schrenkii* Regel, 1875). There are few species endemic to Kashmir and Uttarakhand (e.g. *A. gilgiticum* F.T. Wang et Tang, 1937 which is also endangered, *A. stracheyi* Baker, 1874 and *A. negianum* A. Pandey, K.M. Rai, Malav et S. Rajkumar, 2021) (Pandey et al. 2021). Rest of the species occupy the temperate habitats of north-eastern hill region (e.g. *A. fasciculatum* Rendle, 1906, *A. hookeri* Thwaites, 1864, *A. macranthum* Baker, 1874, *A. platyspathum* Schrenk, 1841, *A. prattii* C.H. Wright, 1903, *A. rhabdotum* Stearn, 1960, *A. sikkimense* Baker, 1874) while some wild or semi-wild species (*A. przewalskianum* Regel, 1875, *A. tuberosum* Rottler et Sprengel, 1825, *A. victorialis* Linnaeus, 1753, *A. wallichii* Kunth, 1843) occur in the western and eastern Himalayan regions.

Chromosome counts

The chromosome counts and karyotype details are known perhaps in 33 and 25 species, respectively (Table 1, Fig. 1). The prominent base number (x) is 8, irrespective of the subgenera, sections or the distribution pattern. Some western Himalayan species which are still not assigned to any of the subgenera (e.g. *A. atropurpureum*, *A. caesioides*, *A. consanguineum*, *A. ascalonicum* Linnaeus, 1756, *A. blandum* Wall., 1832, *A. hypsistum* Stearn, 1960) and endemic *A. stracheyi* have x=8. Divergent numbers such as x=7, 10 and 11 are found in the Indian species of the subgenus *Amerallium* (Table 1) which also justifiy their inclusion in a separate subgenus (Peruzzi et al. 2017). Chromosome number has not been studied in the newly discovered *A. negianum* of *Rhizirideum*, sect. *Eduardia* (Pandey et al. 2021), which together with its close relative *A. przewalskianum* of sect. *Caespitosoprason* (Pandey et al. 2021) not studied from the territory of India, needs to be investigated. Similarly, *A. loratum*, *A. auriculatum*, *A. rhabdotum* and an endemic *A. gilgiticum* still are not assigned to any of the subgenera, and any cytological information is also missing. The meiotic studies in some species have shown various configurations like multivalents or univalents and occasional irregularities as in *A. chinense* G. Don, 1827 (Gohil and Koul 1973, 1981), *A. hookeri* (Sharma et al. 2011), *A. roylei* (Sharma and Gohil 2003, 2011a; Kohli and Gohil 2011), *A. rubellum* M. Bieb., 1808 (Khoshoo and Sharma 1959; Koul et al. 1971) and *A. tuberosum* (Gohil and Koul 1983; Sharma and Gohil 2004, 2013a, b). In case of tetraploid *A. ampeloprasum* Linnaeus, 1753 (as *A. porrum* Linnaeus, 1753 in many studies), 16 bivalents were recorded regularly with complete absence of any multivalent (Koul and Gohil 1970b; Ved Brat and Dhingra 1973; Gohil and Koul 1977; Pandita and Mehra 1981a; Stack and Roelofs 1996). In this species, some peculiar features like appearance of bivalents in metaphase I instead of quadrivalents, localized chiasmata at pericentromeric regions have been reported (Levan 1940; Koul and Gohil 1970b; Stack and Roelofs 1996). Considering the incidence of vivipary and hybridization in *A. cepa* (Singh et al. 1967; Langer and Koul 1983; Puizina and Papea 1996), thorough meiotic analysis of the agriculturally important species (*A. cepa*, *A. sativum*, etc.) would be a significant aspect of future revision.

Ploidy and genome size

The greatest variation in ploidy has been observed in *A. tuberosum* (subgenus *Butomissa*), *A. przewalskianum* (subgenus *Rhizirideum*), *A. chinense* G. Don, 1827 (subgenus *Cepa*) and *A. rubellum*, *A. ampeloprasum*, *A. griffithianum* (subgenus *Allium*) (Table 1). Polyploidy is reported in almost all subgenera and species. However, Peruzzi et al. (2017) reported absence of polyploidy in subgenus *Anguinum* and emphasized on correlation between chromosome size and ploidy to infer the trend of evolution. Any such correlation for Indian taxa is not possible at this stage due to lack of data for all the species.

Table 1. Chromosome numbers, ploidy and nuclear genome sizes in Indian species of *Allium* of Amaryllidaceae (Tribe Allieae, Subfamily Allioideae, sensu APG IV 2016).

Subgenus/ section	Species (syn.)	Chromosome number			Ploidy	4C DNA value in diploid/ polyploid nuclei (pg)	Genome size in diploid/ polyploid (pg)		References
		Basic (x)	Gametic (n)	Zygotic (2n)			1C	1Cx	
Amerallium/ Bromatorrhiza!	***A. fasciculatum* Rendle** (*A. gageanum*)	10[a]	–	20[b], 40[c]	Diploid[d], Tetraploid[e]	–	–	–	[a, b, d](Xu et al. 1998; Li et al. 2017), [b](Huang et al. 1995), [c, e](Dutta et al. 2015)
Amerallium/ Bromatorrhiza*	***A. hookeri* Thwaites** (*A. tsoongii*)	–	–	22[a], 33[b], 44[c]	–	63.24 (diploid, Feulgen cytophotometry)[d]	15.81 (diploid)[d]	15.81[d]	[a](Sen 1974a; Tang et al. 2005; Sharma et al. 2011), [a, b, c](Huang et al. 1995), [a, c](Phuong et al. 2010), [a, d](Ohri et al. 1998; Ohri and Pistrick 2001)
Amerallium/ Bromatorrhiza!	***A. macranthum* Baker** (*A. oviflorum* Regel, *A. simethis* H.Lev.)	–	14[a]	14[b], 28[c]	–	–	–	–	[a](Levan 1934), [b, c](Huang et al. 1995; Tang et al. 2005)
Amerallium/ Bromatorrhiza*!	***A. wallichii* Kunth.** (*A. bulleyanum* Diels, *A. caeruleum* Wall.)	7[a]	-	14[b], 28[c], 32[d]	Diploid[e], Tetraploid[f]	64.98 (diploid, Feulgen Cytophotometry)[g], 121.79 (tetraploid, Feulgen Cytophotometry)[h], 119.13 (tetraploid, Feulgen microdensitometry)[i]	16.24 (diploid)[g], 30.45 (tetraploid)[h]	16.24[g], 15.22[h]	[a, b, c, e, f](Huang et al. 1995), [c, f, i](Labani and Elkington 1987), [d](Ved Brat 1965), [a, b, c, e, f, g, h](Ohri et al. 1998), [a, b, c, e, g, i](Ohri and Pistrick 2001)
Anguinum/ Anguinum*	***A. prattii* C.H.Wright** (*A. cannifolium* H. Lev., *A. ellipticum* Wall et Kunth)	8[a]	16[b]	16[c], 32[d]	Diploid[e], Tetraploid[f]	–	–	–	[a](Lu et al. 2017), [a, c, e](Tang et al. 2005), [b](Kurosawa 1966), [c, d, e, f](Chunying et al. 2000)
Anguinum/ Anguinum!	***A. victorialis* L.** (*A. anguinum* Bubani, *A. reticulatum* St.-Lag.)	8[a]	8[b]	16[c], 32[d], 36[e]	Diploid[f], Tetraploid[g]	81.00 (diploid)[h], 86.42 (diploid, Feulgen microdensitometry)[i], 162.02 to 167.10 (Tetraploid, Feulgen cytophotometry)[j]	20.25 (diploid)[h], 21.60 (diploid)[i], 40.5–41.78(tetraploid)[j]	20.25[h], 21.60[i], 20.25–20.89	[a, b, f](Pandita and Mehra 1981a), [c, f](Pandita and Mehra 1981b), [a, c](Mehra and Sachdeva 1976; Lu et al. 2017), [c, f, i](Labani and Elkington 1987), [d, g, j](Ohri et al. 1998), [d, g, j](Ohri and Pistrick 2001), [e](Sen 1973a), [h](Vakhtina et al. 1977)
Melanocrommyum/ Brevicaule #	***Allium chitralicum*** Wang & Tang (*A. badakhshanicum*, *A. pauli*)	–	–	16[a], 32[b]	–	–	34.35 (tetraploid, flow cytometry)[c**]	17.17 (tetraploid, flow cytometry)[c**]	[a](Pedersen and Wendelbo 1966), [b, c**](Gurushidze et al. 2012)
Butomissa/ Butomissa*	***A. tuberosum* Rottler ex Spreng.** (*A. chinense* Maxim., *A. clarkei* Hook.f.)	8[a]	8[b], 16[c], 32[d]	16[e], 32[f], 24[g], 31, 33[h], 48[i], 61–64 [j], 62[k], 64[l]	Tetraploid[m], Hexaploid[n], Octaploid[o], Autotetraploid[p], Autopolyploid[q]	66.80 (tetraploid)[r], 121 (tetraploid)[s], 109.36 (tetraploid, Feulgen cytophotometry)[r], 121.47–123.25 (tetraploid, Feulgen Cytophotometry)[u]	30.36–30.62 (tetraploid)[u]	15.18–15.31[u]	[a, c, f, m, p](Pandita and Mehra 1981a), [a, f, m](Talukder and Sen 2000; Kumar and Thonger 2018), [b](Li et al. 1985), [c, f](Sharma and Gohil 2004), [c, p](Sen 1974b), [f, m, u](Ohri et al. 1998; Ohri and Pistrick 2001), [d](Koul 1963), [e](Yang et al. 1998), [f](Sharma and Gohil 2013b; [f, i, n, q](Sharma and Gohil 2013a), [g](Huang et al. 1985), [h](Gohil and Koul 1973; Gohil and Kaul 1981), [j](Gohil and Kaul 1979; Ohri 1990), [k](Seo 1977), [l](Kojima et al. 1991), [o](Gohil and Kaul 1979), [p](Dutta and Bandyopadhyay 2014), [r](Nanushyan and Polyakov 1989), [s](Walters 1992), [t](Talukder and Sen 1999)

Subgenus/ section	Species (syn.)	Chromosome number			Ploidy	4C DNA value in diploid/ polyploid nuclei (pg)	Genome size in diploid/ polyploid (pg)		References
		Basic (x)	Gametic (n)	Zygotic (2n)			1C	1Cx	
***Butomissa/ Austromontana**!**	***A. oreoprasum* Schrenk**	–	–	16[a], 48[b]	–	–	–	–	[a](Gohil and Koul 1973; Gohil and Kaul 1981), [b](Ved Brat 1965)
Rhizirideum/ Caespitosoprason*	***A. przewalskianum* Regel** (*A. jacquemontii* var. *parviflorum* (Ledeb.) Aswal, *A. junceum* Jacquem. et Baker)	8[a]	–	16[b], 32[c], 64[d]	Diploid[e], Tetraploid[f] Octaploid[g] Autopolyploid[h]	–	–	–	[a, b, e, f](Tang et al. 2005), [c](Gohil and Kaul 1981), [d, g](Xue et al. 2000), [h](Ao 2008)
Allium/ Allium*	***A. ampeloprasum* L.** (*A. adscendens*, *A. porrum* var. *ampeloprasum*)	8[a]	–	16[b], 24[c], 32[d], 40[e], 56[f]	Diploid[g], polyploid[h]/ autotetraploid[i]	48.20 (tetraploid, feulgen cytophotometry)[j], 100.54 (cytometry)[k], 119.64/ 121.15 (tetraploid, feulgen cytophotometry)[l], 119.80 (tetraploid, feulgen cytophotometry)[m]	16.7 (diploid, flow cytometry)[n**], 25.35–27.45 (tetraploid, flow cytometry)[m,n**]	16.7 (diploid, flow cytometry)[n**], 12.67–13.73 (tetraploid, flow cytometry)[m,n**]	[a, b, d, g, h, i, n**](Ricroch et al. 2005), [a, d, h, i](Pandita and Mehra 1981a), [c, e](IPCN), [d, h, i](Maragheh et al. 2019), [d, h, i, k](Arumuganathan and Earle 1991), [d, h, i, l](Labani and Elkington 1987), [d, h, i, m](Ohri et al. 1998; Ohri and Pistrick 2001), [f, h](von Bothmer 1975), [j](Ranjekar et al. 1978)
Allium/ Allium*	***A. sativum* L.** (*A. arenarium* Sadler et Rchb, *A. controversum* Schrad. et Willd.)	8[a]	8[b]	16[c], 12[d]	Diploid[e]	63.00 (diploid)[f], 64.90 (diploid, Feulgen Cytophotometry)[g], 65.40 (diploid)[h], 66.40–69.00 (diploid)[i], 68.20[l], 71.40[m], 73.59–91.80 (diploid, Feulgen Cytophotometry)[j], 120 (diploid, Feulgen Cytophotometry)[k]	15.75 (diploid)[f],16.23 (diploid)[g],16.35 (diploid)[h], 16.6–17.25 (diploid)[i], 17.05[l], 17.85[m], 18.40–22.95[j], 30.0 (diploid)[k]	15.75[f], 16.23[g], 16.35[h], 16.6–17.25[i], 17.05[l], 17.85[m], 18.40–22.95[j], 30.0[k]	[a](Gohil and Koul 1971), [a, c, e](Kumar and Thonger 2018), [b](Koul and Gohil 1970a), [b, k](Cortes et al. 1983), [c, e](Bacelar et al. 2021), [c, e, g](Ohri et al. 1998; Ohri and Pistrick 2001), [d](Sato and Kawamura 1981), [h](Ranjekar et al. 1978), [f](Murin 1976), [i](Chakravarty and Sen 1992), [j](Talukder and Sen 1999), l (Walters 1992), m(Olszewska and Osiecka 1982)
Allium/ Avulsea*	***A. griffithianum* Boiss.** (*A. bahri*, *A.jacquemontii* var. *grandiflorum*)	8[a]	16[b]	16[c], 32[d]	Diploid[e], Tetraploid[f], Autotetraploid[g]	41.15 (diploid, Feulgen cytophotometry)[h]	10.29 (diploid)[h]	10.29[h]	[a, b, d, f](Pandita and Mehra 1981a), [c, e, h](Ohri et al. 1998; Ohri and Pistrick 2001), [f, g](Pandita and Mehra 1981b)
Allium/ Avulsea*	***A. rubellum* M. Bieb.** (*A. albanum* Grossh., *A. leptophyllum* Wall.)	–	16[a]	16[b], 24[c],	Diploid[d], Triploid[e], Tetraploid[f], Numerical hybrid[g], Autopolyploid[h]	–	–	–	[a, f](Koul et al. 1971), [b, d](Abdali and Miri 2020), [c](Gohil and Koul 1973), [e, h](Khoshoo and Sharma 1959), [g](Ved Brat 1967)
***Allium/ Caerulea*!**	***A. jacquemontii* Kunth**	8[a]	8[b]	16[c]	Diploid[d]	–	–	–	[a, b](Pandita and Mehra 1981a), [c](Gohil and Kaul 1981), [c, d](Pandita and Mehra 1981b)
***Reticulatobulbosa/ Reticulatobulbosa*!**	***A. humile* Kunth** (*A. govanianum*, *A. nivale*)	8[a]	8[b]	–	Diploid[c]	–	–	–	[a, b, c](Pandita and Mehra 1981a), [b](Mehra and Sachdeva 1975), [c](Pandita and Mehra 1981b)

Subgenus/ section	Species (syn.)	Chromosome number			Ploidy	4C DNA value in diploid/ polyploid nuclei (pg)	Genome size in diploid/ polyploid (pg)		References
		Basic (x)	Gametic (n)	Zygotic (2n)			1C	1Cx	
***Reticulatobulbosa*/ *Reticulatobulbosa*!**	***A. schrenkii* Regel** (*A. bogdoicola* Regel)	–	–	32[a]	–	–	–	–	[a](Friesen 1985)
Reticulatobulbosa*/ *Sikkimensia*	***A. sikkimense* Baker** (*A. kansuense* Regel, *A. tibeticum* Rendle)	–	–	16[a], 32[b]	–	–	–	–	[a](Mehra and Pandita 1979), [b](Gu et al. 1993)
Polyprason*/ *Falcatifolia*	***A. carolinianum* DC.** (*A. aitchisonii*, *A. obtusifolium*)	8[a]	16[b]	16[c], 32[d]	Diploid[e], Tetraploid[f]	52.90 (diploid, Feulgen cytophotometry)[g]	13.23 (diploid)[g]	13.23[g]	[a](Tang et al. 2005), [b](Kumari and Saggoo 2016), [c, e, g](Ohri et al. 1998; Ohri and Pistrick 2001), [d](Gohil and Kaul 1981), [f](Oyuntsetseg et al. 2013), [d, f](Pandita and Mehra 1981b; Dutta et al. 2015)
Polyprason*/ *Oreiprason*	***A. roylei* Stearn** (*A. lilacinum* Royle et Regel, *A. rubens* Baker)	8[a]	8[b]	16[c]	Diploid[d]	63.00 (diploid)[e], 70.03 (diploid, Feulgen microdensitometry)[f]	15.75 (diploid)[e], 17.51 (diploid)[f]	15.75[e], 17.51[f]	[a, b, c, d](Kohli and Gohil 2011), [b, c, d](Sharma and Gohil 2011a; Kohli and Kaul 2013), [c, d, e, f](Labani and Elkington 1987), [e](Walters 1992)
***Polyprason*/ *Falcatifolia**!**	***A. platyspathum* Schrenk** (*A. platyspathum* subsp. *platyspathum*)	–	–	16[a]	–	–	–	–	[a](Friesen1986; Zakirova and Nafanailova 1988)
Cepa*/ *Cepa*	***A. cepa* L.** (*A. cepa* var. *aggregatum*, *A. cepa* var. *anglicum*)	8[a]	6[b], 8[c]	14[d], 16[e], 24[f]	Diploid[g], Triploid[h]	65.4 (diploid, flow cytometry)[i], 66.40–69.00 (diploid, Feulgen cytophotometry)[j], 67–71.61 (diploid, Feulgen cytophotometry)[k], 67.5 (diploid, flow cytometry)[l]	16.35 (diploid)[i], 16.60–17.25 (diploid)[j], 16.75–17.90 (diploid)[k], 16.87 (diploid)[l], 16.2 (diploid)[m**], 17.18–17.32 (diploid)[n**]	16.35[i], 16.60–17.25[j], 16.75–17.90[k], 16.87[l], 16.2[m**], 17.18–17.32[n**]	[a, e, g](Mancia et al. 2015), [a, m**](Ricroch et al. 2005), [b](Wang and Zheng 1987), [c](Ved Brat and Dhingra 1973; Gohil and Kaul 1980a; Talukder and Sen 2000; Sharma and Gohil 2011b), [e](Rees et al. 1979; Sato 1981; Joshi and Ranjekar 1982; Cortes et al. 1983; Schubert and Wobus 1985; Fuchs et al. 1995; Johnson and Zhatay 1996; Kim et al. 2002), [c](Van't Hof 1965) [e, f, g, h](Puizina and Papea 1996), [e, g](Narayan 1988; Ahirwar and Verma 2015), [e, g, i](Arumuganathan and Earle 1991), [e, l](Ulrich et al. 1988), [e, j](Chakravarty and Sen 1992), [n**](Baranyi and Grielhuber 1999), [k](Talukder and Sen 1999)
Cepa*/ *Annuloprason*	***A. atrosanguineum* Kar. et Kir.** (*A. monadelphum*)	8[a]	–	16[b],32[c]	diploid[d]	–	–	–	[a, b, d](Tang et al. 2005), [b, d](Ved Brat 1965), [c](Zhukova 1967)
Cepa*/ *Annuloprason*	***A. fedschenkoanum* Regel.** (*A. atrosanguineum* var. *fedschenkoanum*)	8[a]	8[b]	16[c]	Diploid[d]	–	–	–	[a, b, d](Pandita and Mehra 1981a), [c, d](Pandita and Mehra 1981b)
Cepa*/ *Sacculiferum*	***A. chinense* G. Don.** (*A. bakeri*, *A. bodinieri*)	8[a]	–	16[b], 24[c], 32[d]	Triploid[e], Tetraploid[f], Segmental allotetraploid[g]	130.86 (tetraploid, Feulgen cytophotometry)[h]	32.7 (tetraploid)[h]	16.35[h]	[a, d, f, i](Ohri et al. 1998), [a, d, f, g, h](Ohri and Pistrick 2001), [b](Katayama 1928), [c, d, e, f](Wufeng et al. 1993), [d](Ohri et al. 1998; Ogura et al. 1999), [d](Dutta and Bandyopadhyay 2014), [g](Gohil and Koul 1981)

Subgenus/ section	Species (syn.)	Chromosome number			Ploidy	4C DNA value in diploid/ polyploid nuclei (pg)	Genome size in diploid/ polyploid (pg)		References
		Basic (x)	Gametic (n)	Zygotic (2n)			1C	1Cx	
Cepa/ Schoenoprasum*	***A. schoenoprasum* L.** (*A. acutum* Spreng., *A. alpinum* (DC.) *Hegetschw.*)	8[a]	8[b]	14[c], 16[d], 24[e], 32[f], 48[g]	Diploid[h]	31.20 (diploid, 79)[i], 33.20 (diploid)[j], 33.80 (diploid)[k], 34.90 (diploid)[l] 37.73(diploid, Feulgen Cytophotometry)[m], 60.66 (tetraploid)[n]	7.8 (diploid)[i], 8.3 (diploid)[j], 8.45 (diploid)[k], 8.72 (diploid)[l], 9.43 (diploid)[m], 15.16 (tetraploid)[n]	7.8[i], 8.3[j], 8.45[k], 8.72[l], 9.43[m], 7.58[n]	[a, b, h](Pandita and Mehra 1981a), [c](Ohri 1990), [d](Dutta and Bandyopadhyay 2014), [d, h, m](Ohri et al. 1998; Ohri and Pistrick 2001), [e](Kurosawa 1979), [f](El-Gadi and Elkington 1977), [g](Pogosian 1997), [h](Pandita and Mehra 1981b), [i](Ranjekar et al. 1978), [j](Anderson et al. 1985), [k](Jones and Rees 1968), [l](Nanushyan and Polyakov 1989), [n](Labani and Elkington 1987)
–	***A. ascalonicum* L.** (*A. carneum*, *A. fissile*)	8[a]	8[b]	16[c]	Diploid[d]	66.32–68.67 (diploid, Feulgen cytophotometry)[e]	16.58–17.16 (diploid)[e]	8.29–8.28[e]	[a](Darlington and Wylie 1955), [b, c](Cortes et al. 1983), [d, e](Talukder and Sen 1999)
–	***A. atropurpureum* Waldst. et Kit.** (*A. nigrum* var. *atropurpureum*)	8[a]	8[b]	16[c],32[d]	diploid[e], tetraploid[f]	112.81 (tetraploid, Feulgen cytophotometry)[g], 113.66 (diploid, Feulgen cytophotometry)[h]	28.2 (tetraploid)[g], 28.45 (diploid)[h]	14.1[g] 28.45[h]	[a, b, c, e](Koul 1966; Pandita and Mehra 1981a), [c, h](Labani and Elkington 1987), [d, f, g](Ohri et al. 1998; Ohri and Pistrick 2001), [c, h](Gurushidze et al. 2012)
–	***A. blandum*** Wall.	–	16[a]	32[b]	Tetraploid[c]	–	–	–	[a, b, c](Mehra and Sachdeva 1976; dGRIP)
–	***A. caesioides*** Wendelbo (*A. kachrooi*)	–	8[a]	16[b]	Diploid[c]	–	–	–	[a, b, c](dGRIP), [a, c](Pandita and Mehra 1981a), [b](Gohil and Kaul 1980a)
–	***A. consanguineum* Kunth**	8[a]	8[b]	16[c]	Diploid[d]	–	–	–	[a, b, d](Pandita and Mehra 1981a), [a, b](Gohil and Koul 1971), [c, d](Gohil and Kaul 1980b)
–	***A. hypsistum* Stearn**	–	–	32[a]	–	–	–	–	[a](dGRIP)
–	***A. stracheyi* Baker** (*A. longistaminum* Royle)	8[a]	8[b]	16[c], 14[d], 32[e], 48[f]	Diploid[g]	–	–	–	[a, b, g](Pandita and Mehra 1981a), [c](Pandita and Mehra 1981b), [d](Shopova 1966), [d, e, f](Sen 1974a)

*(Friesen et al. 2006), # (Fritsch et al. 2010), ! (Li et al. 2010), superscripts with the same letters correspond to references from which data are obtained, 1C and 1Cx genome sizes have been calculated from 4C DNA values published in references, ** indicate 1C and 1Cx genome sizes that have been determined following 2C DNA values in corresponding references.

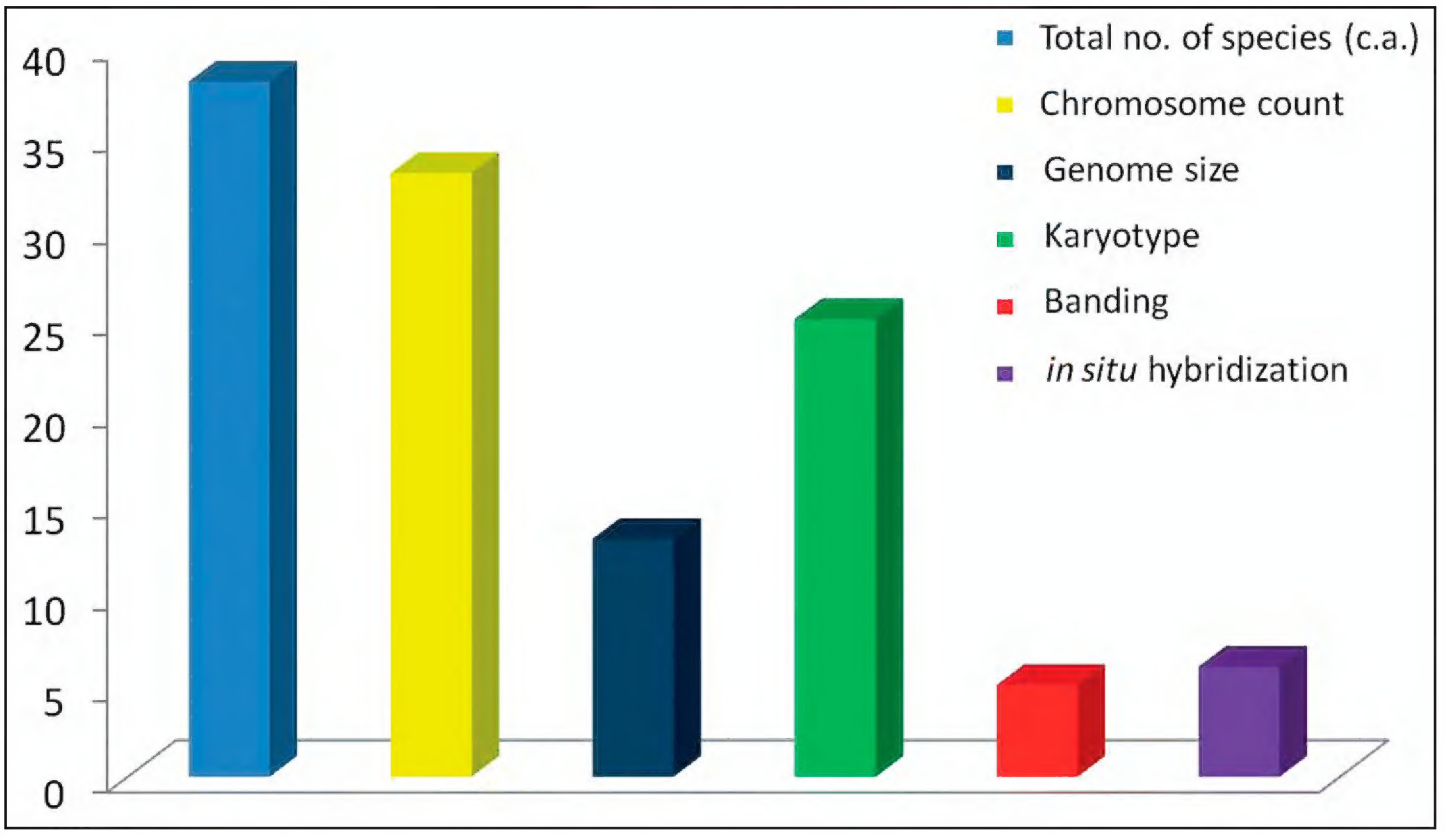

Figure 1. Bar graph showing statistics of cytological reports in the species of *Allium* in India.

Among the diploid species, the range of genome size (Table 1) is from 7.8 pg/1C in *A. schoenoprasum* (subgenus *Cepa*) to 30.0 pg/1C in *A. sativum* Linnaeus, 1753 (subgenus *Allium*). Among the polyploid taxa, the range of genome size (Table 1) is 15.16 pg/1C in *A. schoenoprasum*, 34.35 pg/1C (*A. chitralicum* F.T. Wang et Tang, 1937) to 40.5–41.78 pg/1C in *A. victorialis*. Thus, the lowest values of genome size for the entire array of *Allium* species in India is represented by diploid and polyploid species of *A. schoenoprasum* (subgenus *Cepa*).

The genome size evolution of *Allium* species has been envisaged in relation to growth pattern (dormancy), habitat preference and evolutionary history of the subgenera and sections (Ohri et al. 1998). The authors suggested an overall lack of correlation between genome size and chromosome numbers, although continuity in variation was particularly evident in few species. The present review has showed a 2.25-fold (diploid) or 2.43-fold (tetraploid) difference in genome size in the species occurring in India, although the base number (x) is predominantly 8.

Karyotype features

The karyotype features are known in 8 subgenera and 14 sections of *Allium* species occurring in India (Fig. 1). The majority of species are characterized by metacentric chromosomes except for subgenus *Amerallium* with predominantly submetacentric chromosomes (Table 2). One pair of chromosomes with subterminal constriction has been the characteristic of some species such as *A. cepa* (Sato1981), *A. blandum*, *A. stracheyi* and *A. victoralis* (Mehra and Sachdeva 1976).

Table 2. Karyotype features and molecular chromosomal landmarks in species of *Allium* (Amaryllidaceae, Subfamily Allioideae, Tribe Allieae, sensu APG IV 2016) occurring in India.

Subgenera/ sections	Species	Karyotype		Heterochromatin banding (Giemsa/ Fluorochrome/others)	rDNA/ telomeric/ other signals		References
		Chromosome morphology	SAT or NORs/ 2n		No. of signals/2n	Features	
***Amerallium/ Bromatorrhiza*!**	*A. fasciculatum* Rendle	Majorly submetacentric, few telocentric and metacentric[a]	4[b]	–	–	–	[a, b](Xu et al. 1998; Dutta et al. 2015; Li et al. 2017)
Amerallium/ Bromatorrhiza*	*A. hookeri* Thwaites	Majorly submetacentric, few metacentric[a]	2[b]	–	–	–	[a, b](Sharma et al. 2011)
***Amerallium/ Bromatorrhiza**!**	*A. wallichii* Kunth.	Majority submetacentric[a]	2[b]	–	–	–	[a, b](Huang et al. 1995)
Anguinum/ Anguinum*	*A. prattii* C.H.Wright	Majority metacentric[a]	2[b]/4[c]	–	–	–	[a, b](Tang et al. 2005), [a, b, c](Chunying et al. 2000)
***Anguinum/ Anguinum*!**	*A. victorialis* L.	Majority metacentric[a] or sub–metacentric[b]	2[c]	–	–	–	[a](Pandita and Mehra 1981b), [b, c](Mehra and Sachdeva 1976)
Butomissa/ Butomissa*	*A. tuberosum* Rottler et Spreng.	Majority metacentric[a] or submetacentric[b,c]	3[d]/ 4[e] / 6[f]	–	5S:4–6[g]	5S: proximal and intercalary[h]	[a](Kumar and Thonger 2018), [a, c](Talukder and Sen 2000), [a, c, d, e](Sharma and Gohil 2013b), [a, b](Sharma and Gohil 2013a), [g, h](Do and Seo 2000)
Rhizirideum/ Caespitosoprason*	*Allium przewalskianum* Regel	Majority metacentric chromosomes[a]	2[b]	–	–	–	[a, b](Tang et al. 2005)
Allium/ Allium*	*A. ampeloprasum* L.	Majorly metacentric, few sub–metacentric[a], few subacrocentric[b]	8[c]	Interstitial C– bands colocalized to silver stained regions in 8 active NORs[d], 8 $CMA3^{+}/DAPI^{-}$ bands colocalized to silver stained regions and 35S rDNA sites in NORs[e]	35S:8, 5S: 13 (polymorphic)[f]	35S: interstitial (4) and pericentromeric (4) in short arms[g], 5S: interstitial/ pericentromeric, non–coloclaized to 35S except in one chromosome of 8[th] pair where it flanks 35S site[h]	[a, c, e, f, g, h](Maragheh et al. 2019), [b, c](Koul and Gohil 1970b), [b, c, d](Stack and Roelofs 1996)
Allium/ Allium*	*A. sativum* L.	Majority metacentric[a]	2[b]/ 4[c]/ 6[d]/ 4–8[e]	C–Bands: nucleolar[f], telomeric and interstitial[g], centromeric (2 pairs)[h]; N–bands: nucelolar (4)[i]; Active NORs (AgNORs):2, occasionally4[j]; $CMA^{+}/DAPI^{-}$ bands: 4–6[k]	5S: 4[l], 6[m]; 45S and 5S rDNA localized[n]; telomeric signals in all chromosomes[o]; numerous satellite signals[p]	telomeric signals distal[q], satellite signals sub–telomeric and interstitial[r]	[a](Kumar and Thonger 2018), [a, c](Talukder and Sen 2000), [a, k](Bacelar et al. 2021), [b](Koul and Gohil 1970a), [d, f, g](Cortes et al. 1983), [e, g, h, j](Yuzbasioglu 2004), [i](Cortes and Escalza 1986; Wajahatullah and Vahidy 1990), [l](Do and Seo 2000), [m](Lee et al. 1999; Son et al. 2012), [n](Adams et al. 2001), [o, p, q, r](Peška et al. 2019)
Allium/ Avulsea*	*A. griffithianum* Boiss.	Majorly metacentric[a]		–	–	–	[a](Pandita and Mehra 1981b),
Allium/ Avulsea*	*Allium rubellum* M. Bieb.	Majority metacentric to sub–metacentric[a]	2[b]/ 6[c]/ 8[d]	–	–	–	[a, b](Abdali and Miri 2020), [a, c](Koul et al. 1971), [a, d](Khoshoo and Sharma 1959)
***Allium/ Caerulea*!**	*A. jacquemontii* Kunth	Majority metacentric[a]	–	–	–	–	[a](Pandita and Mehra 1981b)

Subgenera/ sections	Species	Karyotype		Heterochromatin banding (Giemsa/ Fluorochrome/others)	rDNA/ telomeric/ other signals		References
		Chromosome morphology	SAT or NORs/ 2n		No. of signals/2n	Features	
Reticulatobulbosa/ Reticulatobulbosa!	*A. humile* Kunth	Majority metacentric[a]	–	–	–	–	[a](Pandita and Mehra 1981b)
Polyprason/ Oreiprason*	*A. roylei* Stearn	Majority metacentric[a] or sub–metacentric[b]	2[c]	–	–	tyr-FISH mapping of bulb alliinase gene[d]	[a, b, c](Sharma and Gohil 2008), [c](Kohli and Gohil 2011), [d](Khrustaleva et al. 2019)
Polyprason/ Falcatifolia*	*A. carolinianum* DC.	Majorly metacentric, few sub–meta– or sub–telocentric[a]	2[b]	–	–	–	[a, b](Pandita and Mehra 1981b; Tang et al. 2005; Dutta et al. 2015;)
Cepa/ Cepa*	*A. cepa* L.	Majority metacentric, few submetacentric[a]	1[b], 1–2[c], 1–4[d], 2[e], 2–4[f]	C–Bands: telomeric[g], intercalary[h], distal[i], centromeric and at satellites[j]; heterochromatic CMA/DAPI/ AMD bands at NORs and telomeres[k]	18S–5.8S–25S rDNA loci: 2–4[l], 45S rDNA loci: 3[m], 4[n], 4–5[o], 5[p]; 5S rDNA loci: 2[q], 4[r]	Variable rDNA sites[s]; distal 45S rDNA loci colocalized with telomeric tandem repeat[t] and non–colocalized to 5S loci[u]; 5S loci proximal and distal[v] or interstitial[w]; tyrFISH (with allinase, CHS–B and EST markers) reveal chromosome evolution[z]	[a](Fiskesjo 1975; Sulistyaningsih et al. 2002; Ahirwar and Verma 2014), [a, d, g](Sato 1981), [a,e](Talukder and Sen 2000), [a, f](Battaglia 1957), [b](Bozzini 1964), [c, g, h, j](Puizina and Papea 1996), [e,k](Kim et al. 2002), [e, o, q, s, u, w](Mancia et al. 2015), [g](Ghosh and Roy 1977), [i](Tanaka and Taniguchi 1975), [l](Schubert and Wobus 1985), [m](Fu et al. 2019), [n](Do et al. 2001), [p](Ricroch et al. 1992), [r](Shibata and Hizume 2002), [t](Fajkus et al. 2016), [v](Shibata and Hizume 2002), [z](Khrustaleva et al. 2019)
Cepa/ Annuloprason*	*A. atrosanguineum* Kar. et Kir.	majorly metacentric[a]	2[b]	–	–	–	[a, b](Tang et al. 2005)
Cepa/ Annuloprason*	*A. fedschenkoanum* Regel.	Majority metacentric chromosomes[a]	–	–	–	–	[a](Pandita and Mehra 1981b)
Cepa/ Sacculiferum*	*A. chinense* G. Don.	Majority sub– metacentric[a] or submetacentric[b]	2–4[c]	–	–	–	[a](Ogura et al. 1999), [a, c](Sen 1973b), [b, c](Gohil and Koul 1981)
Cepa/ Schoenoprasum*	*A. schoenoprasum* L.	Majority metacentric[a]	1–6[b]	C–bands[c]	5S: 4[d]	5S: interstitial in chromosome 6[e], tyr–FISH of alliinase reveal chromosome evolution[f]	[a](Pandita and Mehra 1981b; Cai and Chinnappa 1987), [a, b](Dutta and Bandyopadhyay 2014), [a, c](Tardif and Morisset 1992), [d, e](Shibata and Hizume 2002), [f](Khrustaleva et al. 2019)
–	*A. ascalonicum* L.	metacentric to sub–metacentric[a]	2[b]	Distal C bands in all chromosomes[c]	–	–	[a, b](Darlington and Haque 1955; Talukder and Sen 2000), [b](Darlington and Wylie 1955), [b, c](Cortes et al. 1983), [c](Seo and Kim 1975)
–	*A. atropurpureum* Waldst. et Kit.	Majorly nearly metacentric and few submetacentric[a]	–	–	–	–	[a](Pandita and Mehra 1981b)
–	*A. blandum* Wall.	metacentric[a]	–	–	–	–	[a](Mehra and Sachdeva 1976; Pandita and Mehra 1981b)
–	*A. consanguineum* Kunth	Majority metacentric or sub–metacentric chromosomes[a]	2 (interstitial)[b]	–	–	–	[a](Mehra and Sachdeva 1976), [a, b](Pandita and Mehra 1981b)
–	*A. stracheyi* Baker	Majority metacentric[a] or sub–metacentric[b]	–	–	–	–	[a](Pandita and Mehra 1981b), [b](Mehra and Sachdeva 1976)

*(Friesen et al. 2006), # (Fritsch et al. 2010), ! (Li et al. 2010), superscripts with the same letters correspond to references from which data are obtained.

The predominance of metacentric chromosomes and symmetric nature of karyotypes is in accordance with earlier studies (Peruzzi et al. 2017). However, few species show a tendency for asymmetry (*A. atrosanguineum*, *A. carolinianum*, *A. griffithianum*, *A. fasciculatum*) and some fall into 2A (*A. chinense*, *A. przewalskianum*) or 2B category (*A. schoenoprasum*, *A. tuberosum*) in Stebbins' index.

Presence of B-chromosomes has been reported in 97 species of *Allium* (Vujošević et al. 2013) belonging mostly to *Allium*, *Cepa* and *Rhizirideum* subgenera (Peruzzi et al. 2017). Among the species found in India, Sharma and Iyengar (1961) first reported the occurrence of B-chromosomes (2–10 in number) in diploid population of *A. stracheyi* and not in the polyploid populations. The B-chromosomes were found to occur in pollen mother cells as well as in pollen grains of *A. stracheyi* (Sen 1974c). However, Mehra and Sachdeva (1976) reported 2n=16 in *A. stracheyi* collected from the Valley of Flowers with no B-chromosome. One or two B-chromosome(s) were reported in *A. ascalonicum* (Bartolo et al. 1984), *A. ampeloprasum*, (subgenus *Allium*) (Khazanehdari and Jones 1996), *A. prattii* (subgenus *Anguinum*) (Chunying et al. 2000), *A. przewalskianum* (subgenus *Rhizirideum*) (Ao 2008; Xie-Kui et al. 2008) while many B-chromosomes (1–10) were recorded in *A. schoenoprasum* (Halkka 1985; Cai and Chinnappa 1987; Tardif and Morisset 1992) and in *A. stracheyi* (subgenus *Cepa*) (Sharma and Aiyangar 1961; Shopova 1966; Pandita and Mehra 1981b).

Nucleolus organizer regions or NORs are significant markers for chromosome identification. Among the species considered presently, NORs/ satellite-bearing chromosomes often show infra-specific or cultivar-specific differences particularly in *A. cepa*, *A. sativum* and *A. tuberosum* (Table 2).

In case of subgenus *Allium*, eight active NORs have been shown in *A. ampeloprasum* by C- banding, $CMA3^{+}/DAPI^{-}$ banding, AgNOR staining and FISH (Table 2). In *A. sativum* secondary constrictions were observed in two to even six chromosomes by C and N banding (Ghosh and Roy 1977; Roy 1978; Cortes et al. 1983), in addition to showing population specific differences (Roy 1978). NORs were also confirmed in four chromosomes by N banding (Cortes and Escalza 1986; Wajahatullah and Vahidy 1990). Recently, two pairs of chromosomes with secondary constrictions were reported in some Brazilian accessions of *A. sativum* of which one pair was suggested to contain intercalary NOR (Bacelar et al. 2021). CMA banding method was used to show the infraspecific heterochromatin variability of nucleolar (proximal) and non-nucleolar (distal and proximal) CMA bands in the Brazilian garlic accessions for their identification. This study remains to be done in case of Indian cultivars.

Allium cepa varieties with different ploidy levels (e.g. *A. cepa* var. *viviparum*, then supposed to be a hybrid between *A. cepa* and *A. fistulosum* Linnaeus, 1753) (Singh et al. 1967; Langer and Koul 1983; Puizina and Papea 1996) show variable number of satellited chromosomes (Bozzini 1964; Singh et al. 1967; Koul and Gohil 1971; Langer and Koul 1983; Puizina and Papea 1996). Many of the conventional staining and C-banding studies showed the presence of two satellite chromosomes in *A. cepa* (Ved Brat and Dhingra 1973; Fiskesjo 1975; Bhattacharyya 1976; Talukder and Sen 2000). Application of differential staining with sequence specific fluorochromes elucidated two NORs in *A. cepa* (Kim et al. 2002). However, reports

claiming variable numbers of NORs (Battaglia 1957; Sato 1981; Puizina and Papea 1996) could not be ruled out. With the application of silver staining, 1–4 active NORs in the satellite region were observed (Sato 1981) while variable number of NORs (2–5) was elucidated by 45S-rDNA hybridization (Table 2). The 45S rDNA sites are distally located and found to co-occur with telomeric tandem repeats (18S). The 5S rDNA loci are reported to range from 2–4 and do not co-occur with the 45S rDNA site.

One interesting feature is that satellites occur mostly in the short arms except for some cases in the subgenera *Allium* and *Amerallium* (Peruzzi et al. 2017). The same phenomenon has been found to exist in case of *A. cepa*, *A. sativum* and *A. ampeloprasum* (Kim et al. 2002; Maragheh et al. 2019; Bacelar et al. 2021). However, the localization of satellites in the species of *Amerallium* and other subgenera of Indian occurrence opens interesting scope of future study. The major difference between subgenera *Allium* and *Cepa* lie in the localization of the NORs rather than numbers of rDNA loci. The NORs are interstitial in *Allium* and distal in *Cepa* (Fig. 2) as confirmed by heterochromatic CMA banding, Ag-NOR staining as well as rDNA FISH (Kim et al. 2002; Fajkus et al. 2016; Maragheh et al. 2019; Bacelar et al. 2021).

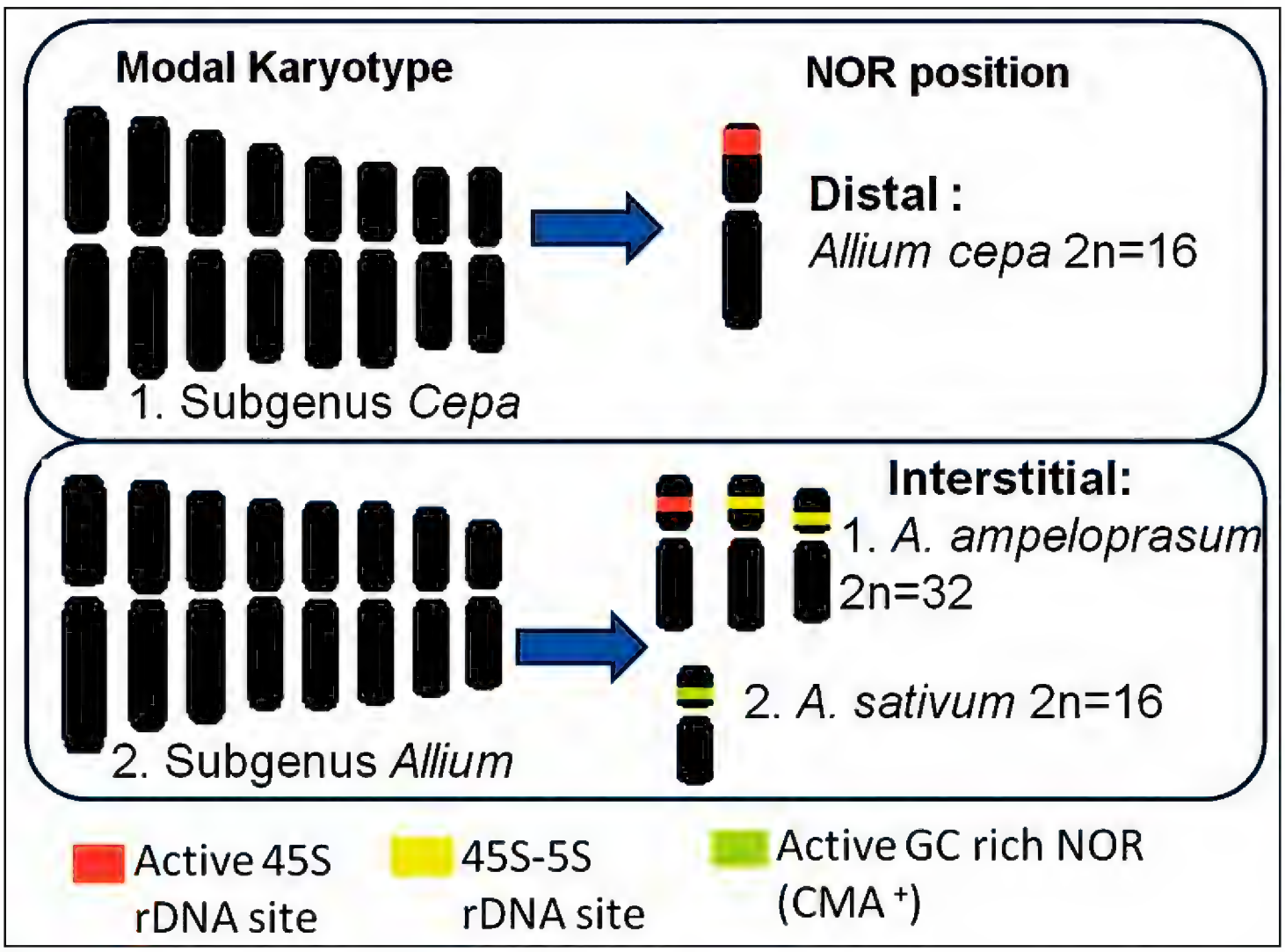

Figure 2. Diagram showing NOR landmarks based on globally published reports in the three species of the genus *Allium* occurring in India. The modal karyotypes for subgenera are adopted and modified after Peruzzi et al. (2017). Diagrams showing NORs are modified after the published reports on *A. ampeloprasum* (as *A. porrum* in Maragheh et al. 2019), *A. sativum* (Bacelar et al. 2021) and *A. cepa* (Fajkus et al. 2016).

Chromosome specialization in *A. cepa*

Telomeres and rDNA loci are the two especially variable features of *A. cepa* chromosomes. Many authors have previously argued that genomic rearrangements are responsible for positional variations of 45S rDNA loci in *A. cepa* (Ricroch et al. 1992; Do et al. 2001; Mancia et al. 2015). The rDNA sequences have been found to contain Copia-like retroelements in *A. cernuum* Roth, 1798 that were dispersed via homogenization mechanisms (Fajkus et al. 2016). The rDNA loci in *A. cepa* have been observed to co-occur with telomeric repeats although telomeres evolved independently of rDNA sequences (Fajkus et al. 2016).

The plant telomere was once thought to be composed of *Arabidopsis* Heynhold, 1842 prototype TTTAGGG repeats (Richards and Ausubel 1988). Exception to this was observed in Asparagales, where an 80 million years old mutation gave rise to human type (TTAGGG) repeat in the family Iridaceae (Adams et al. 2001; Weiss and Scherthan 2002; Sýkorová et al. 2003) and subfamily Allioideae (Sýkorová et al. 2006). The genus *Allium* is different from all other subfamilies of Amaryllidaceae and also other plant groups in terms of the unique telomere sequence. The telomeric sequence $(TTATGGGCTCGG)_n$ surfaced long back (Fuchs et al. 1995) and is neither *Arabidopsis* nor human type. The sequence has been found to be conserved in *Allium*, probing for monophyletic origin of this genus (Fajkus et al. 2016). The telomeres of land plants, including the unique ones like that of Amaryllids, have received less attention (Peska and Garcia 2020). For example, telomeric repeat in *Arabidopsis thaliana* (Linnaeus, 1753) Heynhold, 1842 is a Pol III transcribed lncRNA (Fajkus et al. 2019). Hence, the *Allium* and non-*Allium* taxa of Amaryllidaceae provide excellent scope for studying telomere evolution in eukaryotes.

Recent updates on cytogenetic relationships

A robust phylogenetic analysis supported by genome size and karyotype parameters was found to elucidate the evolution of Gilliesieae of Allioideae (Pellicer et al. 2017). The phylogenetic background of the genus *Allium* has paved way for refinement of classification, inter-species relationships and cytogeographic evolution (Friesen et al. 2006; Gurushidze et al. 2007, 2008; Fritsch et al. 2010; Li et al. 2010, 2017; Abugalieva et al. 2017; Herden et al. 2016; Huo et al. 2019; Costa et al. 2020). Global sampling of 207 species of *Allium* (Allieae) highlighted the ancestral number (x=8) and the reasons behind symmetric karyotype evolution (Peruzzi et al. 2017).

The utility of cytogenetic mapping remains unparallel to investigate synteny comparison between phylogenetically related species that has been employed to interpret chromosome evolution in *Allium* crop species from Russia (Khrustaleva et al. 2019). The presence of flavonoids and sulphur-containing compounds are responsible for the onion's characteristic flavour and the enzyme alliinase is part of the biosynthesis

(Lancaster and Collin 1981). Recent techniques like ultra-sensitive tyramide-FISH (tyr-FISH) and SteamDrop protocol have facilitated the physical detection of the alliinase as well as chalcone synthase genes along with expressed sequence tag (EST) markers. The bulb alliinase gene was located on the long arm of chromosome 4 in *A. cepa* and *A. schoenoprasum* while the same gene was found in the short arm of chromosome 4 in the related (*A. fistulosum*, *A. altaicum* Pallas, 1773, *A. oschaninii* O. Fedtschenko, 1906, and *A. pskemense* B. Fedtschenko, 1905) and phylogenetically distant species (*A. roylei* and *A. nutans* Linnaeus, 1753) (Khrustaleva et al. 2019). Khrustaleva et al. (2019) proposed a pericentric inversion model for rearrangements in chromosome 4 in line with divergence of *A. cepa* and *A. fistulosum*, responsible for breaking collinearity of the genes controlling flavour and bulb colour. This particular report focussed on genomic kinship and genomic rearrangement among the closely related *Allium* species. Also, the practical benefit of molecular cytogenetic mapping becomes apparent in terms of suitably utilizing the genomic resources for onion breeding. These studies would also help to address genomic relationships among *A. cepa*, *A. schoenoprasum* and *A. roylei*, occurring in India.

Summary and future prospects

Considering the impact of cytogenetic investigation in *Allium* phylogeny at a global scale, it is unfortunate to notice the lack of attention in an Indian context in spite of species abundance. Although *A. cepa* has often been regarded as the common material for cytogenetic analysis and the popular '*Allium cepa* test' (Pathiratne et al. 2015; Bonciu et al. 2018), systematic chromosome analysis is still missing in Indian *A. cepa* as well as other species. The present dataset and existing references are not exhaustive but furnish the prerequisite to search for further chromosomal landmarks (NORs, genome size etc) and complement future phylogenetic studies or cyto-geographical evolution of *Allium*, involving the unexplored wild and endemic species in the subcontinent. The crops, onion and garlic, have been admired from ancient time in global cuisines and Indian culinary practices (c.a. 5000 years ago) and continue to be tremendously important in agriculture and pharmaceutical industries (Rana et al. 2011; Nile and Park 2013). The cultivation of onions is challenged by a number of biotic threats which are the direct or indirect manifestation of the current climatic adversity (Le et al. 2021). Identification of wild relatives of the crop having high resistance is germane to address available genomic sources (Dempewolf et al. 2014), which is necessary for *Allium* crop species of India (Gedam et al. 2021). Interesting discoveries on the 'neodomesticate' western Himalaya taxon *A. negianum* (Pandey et al. 2021) along with other endemic less-known species (*A. stracheyi*, *A. roylei*, *A. wallichii* and *A. przewaliskianum*) are assets of Indian repository in line with global assemblages. The genomic attributes of Indian *Allium* germplasm as outlined in this review, could help strategic upgradation of cultivation practices.

Author contribution

Conceptualization, supervision, project administration and funding: SJ, MML, DO, SRR, SRY, MKD, SNR, RCV. Data Curation and data analysis: BKB, SS, DRC, SDP. Writing and Editing: BKB, SS, DRC, MML, DO, SJ.

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